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# SPATIAL CONTAGIOUSNESS OF CANOPY DISTURBANCE IN TROPICAL RAIN FOREST: AN INDIVIDUAL-TREE-BASED TEST

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*Abstract*. Spatial contagiousness of canopy dynamics—the tendency of canopy disturbances to occur nearby existing canopy openings due to an elevated risk of tree fall around gaps—has been demonstrated in many temperate-zone forests, but only inferentially for tropical forests. Hypothesized mechanisms increasing the risk of tree fall around tropical forest gaps are (1) increased tree exposure to wind around gaps, (2) reduced stability of trees alongside gaps due to crown asymmetry, or (3) reduced tree health around gaps due to damage from prior disturbances. One hypothesized consequence of elevated disturbance levels around gaps would be that gap-edge zones offer relatively favorable prospects for seedling recruitment, growth, and survival. We tested whether disturbance levels are indeed elevated around natural canopy gaps in a neotropical rain forest in French Guiana, and more so as gaps are larger. We followed the fate of 5660 trees >10 cm stem diameter over five years across 12 ha of old-growth forest and analyzed the risk and magnitude of canopy disturbance events in relation to tree diameter and the proximity and size of natural canopy gaps. We found that the cumulative incidence of disturbance over the five-year survey was not significantly elevated around preexisting gaps, and only weakly related to gap size. Also, neither the risk nor the magnitude of canopy disturbances increased significantly with the proximity of gaps. Moreover, canopy disturbance risk around gaps was independent of gap size, while the magnitude of disturbance events around gaps was weakly related to gap size. Tree size was the major driver of disturbance risk as well as magnitude. We did find an elevated incidence of disturbance inside preexisting gaps, but this "repeat disturbance" was due to an elevated disturbance risk inside gaps, not around gaps. Overall, we found no strong evidence for canopy dynamics in this rain forest being spatially contagious. Our findings are consistent with the traditional view of tropical rain forests as mosaics of patches with predictable regeneration cycles.

*Key words: Cox regression; French Guiana; gap dynamics; gap expansion; longitudinal cohort study; repeat disturbance; seedling recruitment; tree damage; tree diameter; tree mortality*.

## INTRODUCTION

Canopy openings formed by the falling of canopy trees are the major cause of spatial variation in light levels in tropical forests (cf. Runkle 1982, Brokaw 1985, Van Der Meer et al. 1998). Rates of formation and closure of different-sized canopy openings are fundamental because they determine the structure and species composition of tropical forest (Strong 1977, White 1979). For example, canopy openings may provide a range of "regeneration niches" that allow tree species with different light requirements to coexist in a spatio-temporal mosaic (Grubb 1977, Denslow 1987, Ashton 1998, Brown and Jennings 1998, Brokaw and Busing 2000, Dalling and Hubbell 2002). Also, canopy disturbances may delay competitive exclusion of tree species from forest communities by reopening the area and providing opportunities for colonization (Andrewartha and Birch 1954, Connell 1978, Brokaw and Busing 2000, Sheil and Burslem 2003).

This paper considers the question of whether canopy disturbances in tropical forest are spatially contagious, i.e., whether disturbances are more likely to occur near existing canopy openings than away from them (Runkle 1991, Young and Hubbell 1991, Yavitt et al. 1995). Here, canopy disturbances are defined as discrete events in time where the forest canopy is opened due to one or more tree falls or limb falls (cf. White and Pickett 1985). Spatially contagious disturbance is fundamentally different from age-dependent disturbance, in which canopy disturbance becomes increasingly likely as a forest patch gets older and its trees get larger (Aubréville 1938, Richards 1952, Whitmore 1982), as well as from spatially random disturbance, in which disturbances occur independently of tree size, patch age, or spatial patterns of previous disturbances. Contagious disturbance produces elevated disturbance levels around canopy gaps, resulting in frequent re-disturbance of gaps ("repeat disturbance"; Runkle 1985*b*) and gap expansion (Foster and Reiners 1986). Spatial conta-

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giousness of canopy disturbance has been demonstrated in many studies of temperate forests (e.g., Foster and Reiners 1986, Tanaka and Nakashizuka 1997, Lin et al. 2004, Worrall et al. 2005), but whether canopy dynamics are spatially contagious also in tropical forest is still not resolved.

The question whether canopy disturbance is contagious in tropical forest is important for several reasons. First, if canopy disturbances tend to recur near the same location, causing frequent repeat disturbance, this increases the variation in the rate at which canopy gaps close. The lag time between disturbances (turnover time; White and Pickett 1985) will be more variable among forest patches than under age-dependent disturbance or even spatially random disturbance. Because this lag time affects forest structure and species composition locally, increased variation would allow a broader range of specialized species to coexist in the system than would disturbances that are randomly distributed in space (Young and Hubbell 1991). Second, if canopy disturbances tend to recur near the same locations, canopy gaps are more predictable in space and time than they would be under random disturbance. Short-lived pioneer species will potentially (if they survive recurring disturbance events) have a longer period to complete their life cycle—including multiple gap episodes—than under age-dependent disturbance or spatially random disturbance (Runkle 1985*b*, Young and Hubbell 1991). Also, if new canopy gaps tend to occur nearby the locations of established pioneer trees, this facilitates colonization of new gaps by these tree species (Grau 2000). Third, if the likelihood of canopy opening is elevated around existing gaps, then a seedling's potential to acquire the light necessary for successful establishment, survival, and growth will be higher in the zone immediately around maturing gaps than in random places in old-growth tropical forest (Schupp et al. 1989). This implies that gap-edge zones are the areas to which shade-intolerant trees should disperse their seeds. A final consequence of spatial contagiousness of canopy disturbance could be that the formation of large gaps can boost disturbance among the surrounding forest and thus push forests into a state of hyperdynamism (Dale et al. 1986, Laurance 1997).

### *Mechanisms of contagious disturbance*

In species-diverse, uneven-aged tropical forest, spatially contagiousness of canopy disturbance may arise from several mechanisms, all of which elevate the risk of tree fall and other major damage for trees around gaps. First, increased wind turbulence and greater wind force inside canopy gaps may elevate treefall risk around gaps (Alexander 1964, Sprugel 1976, Foster and Reiners 1986, Young and Hubbell 1991). As wind forces increase with gap size, this risk should also increase with gap size (Young and Hubbell 1991). Second, trees growing along gaps tend to extend lateral branches toward the light, displacing their crowns into the openings (Young and Hubbell 1991, Young and Perkocha 1994, Muth and Bazzaz 2002). The resulting crown asymmetry may decrease tree stability and produce an elevated risk of tree fall alongside gaps (Foster and Reiners 1986, Young and Hubbell 1991, Young and Perkocha 1994). Gap-bordering trees, i.e., canopy trees whose crowns form the border of a canopy opening, should thus be more likely to fall than trees surrounded by closed canopy (Young and Hubbell 1991). Third, reduced stability and reduced health as a result of damage inflicted during gap formation could increase treefall risk among gap-bordering trees (Putz and Chan 1986). The above mechanisms may be expected to reinforce each other.

On the other hand, there are reasons to expect that contagious disturbance will be less common in tropical rain forest than in temperate-zone forest. First, tropical forests usually are much more species diverse and often more unevenly aged than the temperate-zone forests for which contagiousness has been demonstrated. Heterogeneity in species and age implies that trees exposed to an agent of disturbance will be more heterogeneous in their response. Disturbance agents might be less likely to produce consistent effects. Second, two major mechanisms causing contagious disturbance in temperate-zone forests are probably less important in tropical rain forest. Host-specific diseases or pest outbreaks, a common biotic agent of contagious disturbance in temperate forests (e.g., Rizzo et al. 2000, Worrall et al. 2005), are less likely to play a role in (species-rich) tropical forests, where neighboring individuals tend to be heterospecifics. Fire can be an important cause of contagious disturbance in temperate-zone forests, but only rarely plays a natural role in most tropical rain forests. Third, natural canopy gaps in tropical forests tend to be small compared to the canopy openings in temperate-zone studies that demonstrated contagiousness, which included large, man-made clearings. Because small-scale gaps are expected to less dramatically increase wind exposure, wind (perhaps the most common abiotic agent of disturbance) may play a lesser role in tropical forests.

### *Contagious disturbance in tropical forest*

Few studies have suggested that canopy disturbance in tropical forest is spatially contagious, and most provide only circumstantial evidence. For example, spatial contagiousness of canopy disturbance has been inferred from frequent repeat disturbance of gaps; quadrants with recurrent tree falls were clumped in Mexico (Martinez-Ramos et al. 1988), canopy disturbances were more common among gap-containing quadrants than in quadrants without gaps in Panama (Young and Hubbell 1991), and frequencies of gap re-disturbance were high in French Guiana (e.g., Van Der Meer and Bongers 1996*b*). However, repeat disturbance of gaps can have causes other than an elevated disturbance risk around gaps, such as the staggered breakdown of damaged or dead trees inside gaps. Thus,

although contagious disturbance can cause repeat disturbance, high frequencies of repeat disturbance do not necessarily imply contagiousness of canopy disturbance. Spatial contagiousness of canopy disturbance has also been inferred from aggregated spatial patterns of canopy gaps in Costa Rica (Lawton and Putz 1988), Panama (Yavitt et al. 1995), and Ecuador (Salvador-Van Eysenrode et al. 2000), but these aggregation patterns need not result from an elevated disturbance risk around preexisting gaps. Young and Hubbell (1991) showed that trees around gaps tend to be develop asymmetrical crowns, while Young and Perkocha (1994) showed that crown asymmetry increases treefall risk, but neither study directly tested the inference that trees around gaps actually had an elevated treefall risk. As far as we know, the only direct evidence for contagiousness of canopy disturbance in tropical forests comes from Hubbell and Foster (1986), who found in Panama that the likelihood of canopy disturbance increased as more of the surrounding patches had lower (i.e., disturbed) canopies. Hubbell and Foster concluded that "trees adjacent to gaps ... suffer a greater risk of falling than trees which are surrounded by plants as tall or taller than themselves." On the other hand, studies finding relatively high disturbance levels in old forest (e.g., Brokaw 1982*b*) argue against contagious disturbance. Thus, the evidence for contagious disturbance in tropical forests is not strong.

### *This study*

We studied the canopy disturbance regime in an old-growth tropical rain forest in French Guiana. Our aim was to determine whether canopy disturbance was more common around existing gaps than expected by chance, and more so as gaps were larger. Unlike most previous studies addressing contagiousness, our study was focused on individual trees rather than areas or "patches" (White and Pickett 1985), as all mechanisms that may cause contagious disturbance in tropical forest operate on trees rather than surfaces.

We considered three aspects of canopy disturbance. First, we evaluated the cumulative *incidence* of tree disturbance, i.e., the proportion of the study trees heavily damaged at the end of the survey and the proportion of the study area turned into canopy gap at the end of the survey, in relation to the location and size of canopy gaps at the start of the survey. Second, we analyzed the *risk* of canopy disturbance, i.e., the rate at which trees initiated disturbance events, in relation to tree diameter and the location and size of gaps. Focusing on initiators of disturbance events accounts for the strong spatial dependence of tree damage (disturbance events tend to affect multiple trees simultaneously). Third, we analyzed the *magnitude* (sensu White 1979) of disturbances, i.e., the amount of tree damage caused by a single disturbance event, as a function of the diameter and location of the initiator. Thus, we acknowledge that any elevated canopy disturbance levels can be due to not only an increased disturbance risk, but also to an increased magnitude of individual disturbance events, or to both. Note that an elevated disturbance risk can theoretically be offset by a reduced magnitude of disturbances and vice versa.

We tested the following hypotheses: (1) Canopy disturbance risk is elevated around gaps. Specifically, the rate at which trees initiate disturbance events (1a) increases with decreasing distance to the nearest gap, (1b) is elevated in the "edge zone" of gaps (cf. Schupp et al. 1989), and (1c) is elevated for "gap-bordering trees" (cf. Young and Hubbell 1991); (2) canopy disturbance risk increases with the size of the gap to which trees are exposed; (3) the magnitude of canopy disturbance events is elevated around gaps; (4) the magnitude of canopy disturbance events increases with the size of the gap to which the initiating tree is exposed (cf. Young and Hubbell 1991).

We took into account tree diameter as a covariate in our tests of these hypotheses because tree size can be a major determinant of disturbance in old forests (Busing 2005). Especially large canopy trees may have high mortality (Lorimer et al. 2001, Busing 2005), and gap size is known to increase with tree size (e.g., Brokaw 1982*b*). However, the combined effects of tree size on canopy disturbance levels are not fully understood (Busing 2005).

## Methods

### *Study site*

Data were collected in the Nouragues Biological Reserve, an old-growth neotropical lowland rain forest site in French Guiana, 100 km south of Cayenne, at 4°05′ N, 52°40° W. The area ranges 60–120 m above sea level (asl) with the exception of an up to 450 m high granitic outcrop complex (inselberg). Annual precipitation averages 2990 mm, with a distinct dry season from September to November and a short dry period around February–March (Grimaldi and Riera 2001). Field work was carried out at the "petit plateau," a relatively flat and homogenous area of ~35 ha at 90–110 m asl. The area has shallow, well-drained clayey to sandy-clayey ferralitic soils on weathered granite and crystalline bedrocks (Grimaldi and Riera 2001). The dominant tree families are Caesalpiniaceae, Lecythidaceae, Mimosaceae, and Sapotaceae (Poncy et al. 2001). Bongers et al. (2001) provide extensive details on this forest.

### *Tree and gap surveys*

We recorded canopy disturbance in relation to the proximity of gaps across 400 × 300 m (12 ha) of old-growth forest during five years by following the fate of all living trees >10 cm stem diameter at breast height (dbh; 1.3 m or above buttresses). Trees were mapped, dbh was recorded to the nearest centimeter, and all existing canopy openings were located and mapped in June–August 1992 (Van Der Meer and Bongers 1996*b*). We only mapped canopy openings >4 $m^2$ extending

through all levels down to a mean height of 2 m above the ground (cf. Brokaw 1982*a*). For these openings, we mapped the "expanded gap" (Runkle 1985*a*): the polygon connecting the stem bases of all ($\geq$3) trees $>$20 m tall that border the canopy opening with their crowns (henceforth "gap-bordering trees"). In contrast to gaps sensu Brokaw (1982*a*), expanded gaps can still contain trees. For each of these expanded gaps (henceforth "gaps"), we calculated gap size as the area enclosed by the polygon (henceforth "gap contour"). These were the "preexisting gaps" as opposed to "new gaps" that were formed during the study period.

We recorded canopy disturbance in the study area during five full years (1992–1997) by monitoring for major tree damage, one to several times per year. Major tree damage was defined as uprooting or stem snapping (henceforth "tree fall"), loss of a major ($>$10 cm diameter) branch or a significant part of the tree crown (henceforth "limb fall"; Aide 1987), or significant stem inclination. Note that tree damage is not equivalent to "tree mortality"; damage is not necessarily lethal to trees and trees need not break down or fall immediately upon death. Trees at a single location that were damaged simultaneously were grouped in "disturbance events." For each disturbance event, we recorded the date of its occurrence based on our own direct observations or based on the station's logbook in which colleagues recorded new tree falls. If no exact date was available, we estimated the date from the decomposition state of fallen debris, the freshness of snapped wood and uprooted soil, the presence and condition of leaves, and/or the presence and size of re-sprouts. Moreover, for each disturbance, we determined which single tree was the most likely "initiator" (Van Der Meer and Bongers 1996*b*) of the disturbance. The location of this tree defined the location of the disturbance. For each disturbance, we calculated two measures of disturbance magnitude: (1) the total number of trees damaged and (2) only the number of trees fallen (uprooted or stem snapped). If a disturbance event resulted in the formation of a new gap sensu Brokaw (1982*a*) or in the expansion of an existing gap, we mapped the new expanded gap contour, as just described.

For each mapped tree, we calculated the distance to the nearest gap contour. Trees located within gaps had distances with a negative sign. Gap-bordering trees, by definition, had a distance of 0. From these distances, we derived two classifications of tree proximity. In the first classification, we grouped trees into (1) closed forest, trees rooted outside gaps and $>$5 m away from the nearest gap contour; (2) edge zone, trees rooted within 5 m from any expanded gap contour; this category includes all "gap-bordering trees"; and (3) gap center, trees rooted inside gaps and $>$5 m from the nearest gap contour. In the second classification, we grouped trees as (1) "gap-bordering," trees rooted at the expanded gap contour (distance $=$ 0); (2) inside gap, trees rooted within the contours of an expanded gap (distance $<$ 0); and (3) outside gap, trees rooted outside the contours of any expanded gap (distance $>$ 0). The 10 m wide "edge zone" (classification 1) forms the proximity class with elevated canopy disturbance levels under hypothesis 1b, while the "gap-bordering trees" (classification 2) form the proximity class with elevated disturbance levels under hypothesis 1c. By using the distance to the nearest gap as the measure for exposure to gaps, we make the simplifying assumption that only the nearest gap matters for exposure. Because trees may in reality be exposed to multiple gaps, our measures of gap proximity may underestimate exposure to gaps. This underestimation will increase our type I error, i.e., the chance that we wrongfully conclude that there is evidence for contagiousness.

### *Analyses*

We carried out three sets of analyses. First, we used descriptive statistics to explore the cumulative incidence of tree damage and gap formation through the study period in relation to the location and size of preexisting gaps. These analyses show the apparent relationships. Unlike the analyses described later, they are uncorrected for confounding effects of tree size, dependence of tree fates within disturbance events, or temporal changes in gap proximity and gap size during the survey.

Second, we used Cox proportional hazards models (Cox 1972) to analyze the disturbance-risk data, which were essentially waiting times: the time that elapsed until a tree initiated a disturbance event. Our experimental units were individual trees. We tested whether the disturbance risk was elevated for trees near gaps (hypotheses 1a–c) and whether the disturbance risk increased with the size of the gap to which trees were exposed (hypothesis 2). Initial dbh was included as a fixed covariate. To account for increases in trees' exposure to gaps during the study period due to the formation of new gaps, gap proximity and gap size were included as time-dependent covariates, using the counting process method (Anderssen et al. 1993). If a tree remained intact during the entire survey period, the observation was "censored" at the end of the survey period, i.e., it took longer than the monitoring period for the event to occur. If a tree got uprooted or stem-snapped during the monitoring period, the observation was censored at the time of damage, because such a tree could no longer initiate a disturbance event. Hypothesis 1a was tested for trees located outside gaps (including the gap-bordering trees) with distance-to-gap as a continuous variable. Hypotheses 1b and 1c were tested for all trees, with gap proximity classifications 1 and 2, respectively, as a factor. Hypothesis 2 was tested for all trees located in gap centers and gap-edge zones, and was tested with gap size as a continuous variable.

Third, we used generalized linear models (GLM) with Poisson errors to analyze the data on the magnitude of disturbances, i.e., the amount of damage caused by a disturbance event. Here, our experimental units were the

individual disturbance events that occurred during the survey and the individual trees that initiated these. The dbh of the initiator of the disturbance was included as a covariate, as well as the gap proximities and gap sizes of the initiator at the time the event occurred. Effects of gap proximity (hypothesis 3) were evaluated for all disturbances; effects of gap size (hypothesis 4) were evaluated only for disturbances initiated by gap-exposed trees. Additionally, we separately considered those disturbances that were known to be initiated by a tree fall, reasoning that these might have a more consistent damaging effect than disturbances initiated by limb fall.

In all of the above analyses, we excluded the trees and disturbance events that were located <10 m from the edge of study area in order to minimize effects of (unmapped) gaps outside the study area. Trees in this 10-m zone were, however, included in the calculations of disturbance magnitude. We $\log_{10}$-transformed dbh, distance-to-gap, and gap size to normalize the data and also because we were interested in effects of relative differences rather than absolute differences. Gap size and tree distance-to-gap were calculated in ArcView GIS 3.3 and ArcMap 9.2 with the extensions Nearest Features 3.8 (ESRI, Redlands, California, USA), ET GeoWizards 9.7 (ET Spatial Techniques, Pretoria, South Africa), and Hawth's Analysis Tools 3.27 (*available online*).[4] Statistical analyses were done in R 2.6.0 (R Development Core Team 2007), including the R package "survival."

## Results

The total number of living trees ≥10 cm dbh in the study area was 6413 (534 individuals/ha). After exclusion of the 753 individuals located <10 m from the plot edge (gray hatched zone in Fig. 1), the study population amounted to 5660 trees across 10.6 ha. The study area included a total of 70 preexisting canopy gaps and gap complexes, which covered 19.9% of the study area (Fig. 1). Expanded gap sizes ranged from 8 to 1434 $m^2$ (337 ± 286; mean ± SD), implying that there was wide variation in the size of gaps to which trees were exposed.

At the start of the survey, most of the trees were located in closed forest, i.e., >5 m away from the nearest gap contour, but a considerable proportion of the study population was located inside or nearby gaps (Table 1). Tree densities were significantly lower in gap centers than elsewhere (Table 1; chi-square test, $\chi^2_1 = 38.4$, $P < 0.001$), and significantly lower inside gap contours than outside gap contours, even if gap-bordering trees were included in the former class ($\chi^2_1 = 6.2$, $P = 0.013$). Also, dbh was smaller for trees in the gap center than for edge trees and forest trees (Welch two-sample $t$ test, $t_{163} = 11.1$, $P < 0.001$), and smaller for trees inside gaps than for trees outside gaps ($t_{1504} = 12.1$, $P < 0.001$). Furthermore, gap-bordering trees had a larger dbh than all other trees ($t_{501} = 15.0$, $P < 0.001$). These biases in tree density and diameter are likely to be artifacts of the way in which canopy gaps and gap-bordering trees were defined (see *Methods* section). Gap-edge zones and closed forest, however, did not differ significantly in either tree density ($\chi^2_1 = 0.84$, $P = 0.36$) or tree diameter ($t_{4153} = 1.91$, $P = 0.06$).

### *Cumulative incidence of tree damage*

Over the five-year survey, the total number of trees that were heavily damaged totaled 533 trees, or 1.9% per year (Table 1). Most damaged trees were located nearby preexisting gaps (Fig. 2a, open bars), which suggests contagiousness. However, these high frequencies were due to the relatively high number of trees being located in that zone (gray bars), simply because gap-edge zones comprised a relatively large part of the study area. Proportionally, the damage frequency was not significantly elevated for trees in the edge zone of preexisting gaps (Fig. 2b). Instead, the proportion of trees damaged was relatively low in gap-edge zones and relatively high in gap centers and at 35–40 m away from gaps. Moreover, damaged trees were not located significantly closer to preexisting gaps than were non-damaged trees (9.18 vs. 8.52 m; two-sample $t$ test: $t_{615} = 1.41$, $P = 0.16$).

In terms of gap-proximity classes, the cumulative incidence of tree damage was also not significantly elevated for edge trees or gap-bordering trees (Table 1). However, the proportion of the tree population damaged was twice as high for gap-center trees than for edge and forest trees (Pearson's chi-square test with Yates' correction, $\chi^2_1 = 10.8$, $P = 0.001$) and ~40% higher for trees inside gaps than for gap-bordering trees and trees outside gap contours ($\chi^2_1 = 10.3$, $P = 0.001$). Still, the number of trees damaged was entirely proportional to the amount of area covered by each proximity class, both for classification 1 (Pearson's chi-square test with fixed proportions and simulated $P$ values, $\chi^2_2 \leq 2.9$, $P \geq 0.23$) and classification 2 ($\chi^2_1 \leq 1.3$, $P \geq 0.26$).

New gaps that were formed across the five-year survey covered 10.6% of the 12 ha, sometimes overlapping with preexisting gaps. Most of this new gap area was located in the edge zone of preexisting gaps (Fig. 2b), suggesting contagiousness. Again, however, this was due to this zone covering a relatively large proportion of the area. Proportionally, the amount of the edge-zone area turned into gap was relatively small (Fig. 2b, line). The proportion turned into gap was relatively high in gap centers, again indicating frequent gap re-disturbance, but also between 30 and 45 m away from preexisting gaps. Thus, overall, the cumulative incidence of tree damage and gap formation was relatively high inside gaps, indicating elevated (re-)disturbance levels in gaps, but not elevated around gaps, unlike what one would expect if canopy disturbance were spatially contagious.

Finally, the incidence of tree damage showed a positive relationship with gap size. Among the 65 preexisting gaps that were associated with gap-edge

[4] ⟨http://www.spatialecology.com/htools⟩

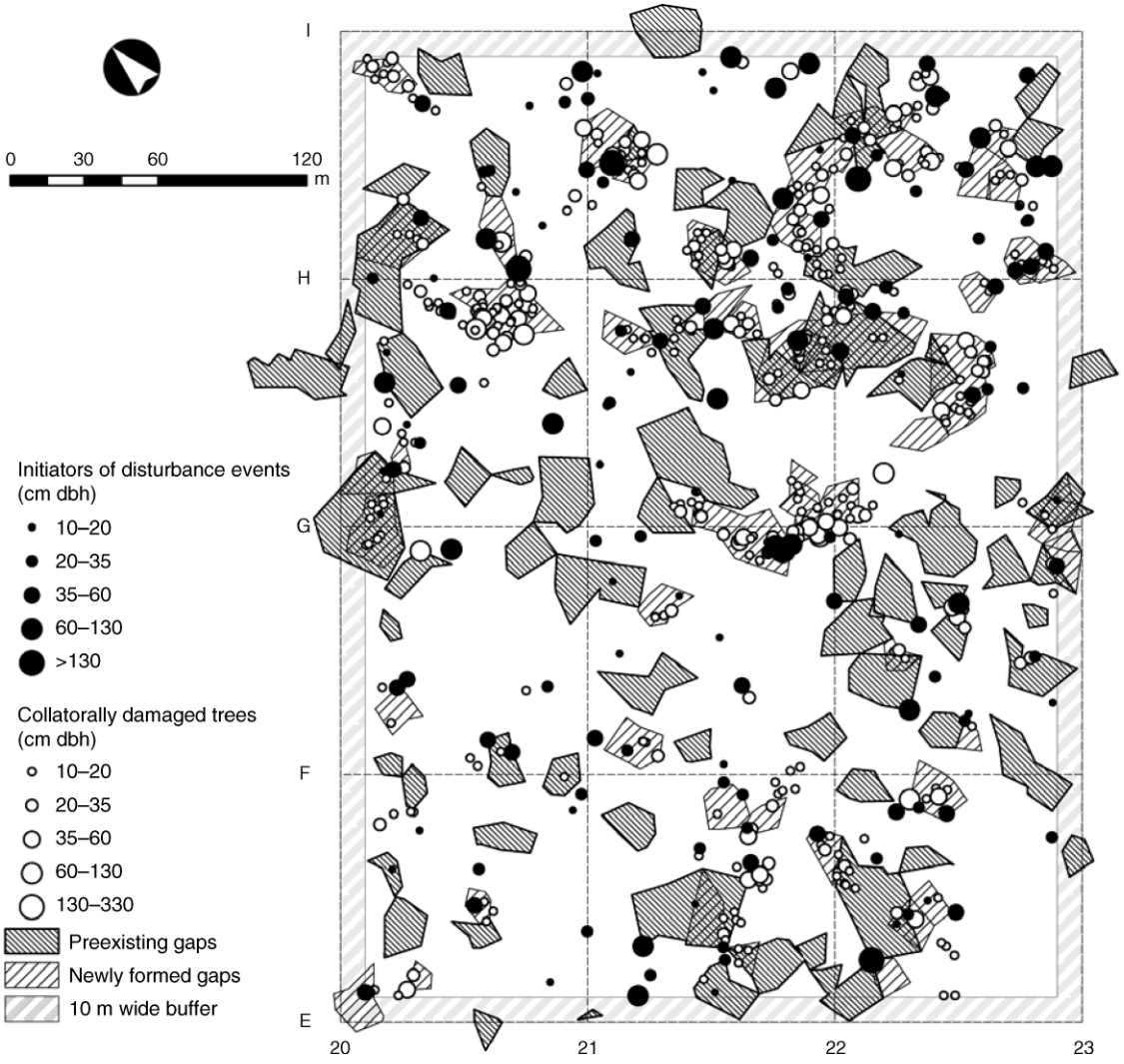


FIG. 1. Spatial distribution of canopy disturbance and canopy gap formation in relation to preexisting canopy gaps across 12 ha of tropical rain forest at Nouragues, French Guiana. Solid circles are trees that initiated a disturbance event; open circles are trees that were damaged. The $100 \times 100$ m grid of trails is coded by letters and numerals along the sides of the figure. The gray and white hatched area around the edges of the figure is a 10 m wide buffer zone that was excluded from the analyses.

trees from the study population, the proportion of gap-edge trees damaged increased significantly with gap size (Fig. 3; weighted logistic regression, $t_{1,63} = 4.66$, $P < 0.001$), but this relationship became nonsignificant when the two largest gaps (>1200 $m^2$) were excluded from the analysis (Fig. 3, dashed line; $t_{1,63} = 1.95$, $P = 0.06$). Among the 26 gaps that had gap-center trees, the proportion of those trees damaged also did not increase with gap size ($t_{1,24} = 1.86$, $P = 0.08$).

### *Disturbance risk*

Our second set of analyses considered the disturbance risk; the rate at which the trees in the study population initiated disturbance events during the survey period. In these analyses, we do take into account the variation in tree diameter as well as the fact that tree proximity to gaps and the size of the nearest gap were time-dependent covariates. That is, we incorporate that the exposure to gaps increased during the survey for 1857 trees (32.8% of the population) due to the formation of new gaps, up to four times per tree. Moreover, we accounted for increases over time in the size of gaps to which trees were exposed, which occurred if newly formed gaps overlapped with existing gaps.

We recorded 172 distinct canopy disturbance events across the study area. Of these events, 33 were initiated by trees outside the study population (three trees located outside the study area, nine dead trees, and 21 trees located in the 10-m buffer zone) and not considered further. Among the study population, we recorded 139 disturbance events, or 2.6 events·$ha^{-1}$·$yr^{-1}$. These events

TABLE 1. Characteristics of the study population and cumulative incidence of tree damage through five years across 10.6 ha of tropical rain forest at Nouragues, French Guiana, for different proximities to preexisting canopy gaps.

| Proximity to gap | Area (ha) | Total area (%) | No. trees | % of all trees | Tree population characteristics | | Cumulative tree damage (%) | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | dbh (cm)† | Density ($ha^{-1}$)‡ | Tree fall | Other tree damage | Total tree damage |
| Classification 1§ | | | | | | | | | |
| Closed forest | 6.1 | 57.2 | 3324 | 58.7 | 22.9[a] (15.5) | 545[a] | 5.3[a] | 4.3[a] | 9.6[a] |
| Gap edge | 4.1 | 38.9 | 2210 | 39.0 | 23.8[a] (18.5) | 539[a] | 4.6[a] | 4.1[a] | 8.7[a] |
| Gap center | 0.4 | 3.8 | 126 | 2.2 | 16.1[b] (6.7) | 315[b] | 12.7[b] | 5.6[a] | 18.3[b] |
| Classification 2§ | | | | | | | | | |
| Outside gap contour | 8.5 | 80.1 | 4459 | 78.8 | 22.1[a] (14.7) | 525[a] | 5.0[a] | 3.9[a] | 8.9[a] |
| Gap bordering | | | 479 | 8.4 | 40.9[b] (27.9) | | 4.0[a] | 5.6[a] | 9.6[a] |
| Inside gap contour | 2.1 | 19.9 | 722 | 12.8 | 17.4[c] (8.6) | 344[b] | 7.5[b] | 5.3[a] | 12.7[b] |
| Total | 10.6 | 100 | 5660 | 100 | 23.1 (16.7) | 534 | 5.2 | 4.2 | 9.4 |

*Note:* Blank cells indicate that this category has 0 area by definition.

† Different characters indicate significant ($P < 0.05$) differences in mean diameter (SD shown in parentheses) among categories (two-sample $t$ tests).

‡ Different characters indicate significant differences in frequency among categories (chi-square tests).

§ Classifications 1 and 2 offset gap-edge zones and gap-bordering trees, respectively, from gaps and closed forest.

were initiated by 134 different trees; in other words, 2.4% of all trees initiated one or more disturbances.

Cox proportional hazards modeling did not reveal a significant increase of disturbance risk with gap proximity, regardless of how gap proximity was defined (Table 2). First, among trees located outside expanded gaps, the disturbance risk did not increase with distance-to-gap (Table 2a), in disagreement with hypothesis 1a. Second, the disturbance risk was significantly elevated for gap center trees (these trees were almost four times as likely to initiate a disturbance event than closed forest trees of similar size), but the disturbance risk was not significantly different between forest trees and edge trees (Table 2b), in disagreement with hypothesis 1b. Third, the disturbance risk did not differ between gap-bordering trees and trees outside the gap contours (Table 2c), in disagreement with hypothesis 1c. Diameter at breast height, in contrast, was a highly significant risk factor for disturbance in all three models: trees were more likely to initiate disturbance events as they were larger.

Gap size was a significant risk factor neither for trees in gap-edge zones nor for gap-bordering trees (Table 3b–c). In other words, gap size did not increase canopy-disturbance risk around gaps, which is in disagreement with hypothesis 2. Even for all gap-exposed trees lumped, the rate at which trees initiated disturbance events did not increase significantly with gap size (Table 3d). Tree diameter, in contrast, was a significant risk factor for trees in gap-edge zones and for gap-bordering trees, but not for gap-center trees.

### *Disturbance magnitude*

Our third set of analyses considered the magnitude of disturbance events that occurred: the amount of damage inflicted on the forest by a single disturbance event. Again, these analyses took into account the variation in diameter among trees as well as changes in tree exposure to gaps during the survey period.

The 139 disturbance events varied widely in their magnitude, which ranged from 1 to 72 damaged trees per event (5.4 ± 11.4; mean ± SD), and 0–72 fallen trees per event (4.0 ± 10.1). Little of this variation was explained by the proximity to gaps of the initiator at the time of the event. GLM of the magnitude of disturbance events, taking into account the initiator's dbh, revealed no significant relationship of disturbance magnitude with distance-to-gap, and no significant differences in disturbance magnitude among proximity classes (Table 4). Disturbance magnitude did show a strong relationship with dbh: events involved more damage as the initiator had a larger diameter. These relationships became stronger if we considered only the disturbances initiated by tree falls, hence excluding limb falls which are less likely to cause damage (Fig. 4). Thus, the magnitude of canopy disturbance was dependent on the initiator's size but not significantly on its proximity to a gap, which is in disagreement with hypothesis 3.

For events initiated by trees located in gap-edge zones, disturbance magnitude increased significantly with gap size, regardless of how magnitude was measured (Table 5, Fig. 5), although this relationship becomes nonsignificant if we exclude the largest gap, both for the number of trees damaged ($F_{1,56} = 1.06$, $P = 0.31$) and the number of tree falls ($F_{1,56} = 0.66$, $P = 0.42$). Disturbance magnitude did, however, consistently increase significantly with the initiator's dbh (Table 5). For events initiated by gap-bordering trees, there was no significant increase of disturbance magnitude with gap size (Table 5). For the subset of events initiated by tree fall of gap-bordering trees, the relationships with gap size and initiator diameter became significantly positive for gap-bordering trees as well, and similar to all events in gap-edge zones. Thus, there was a weak relationship

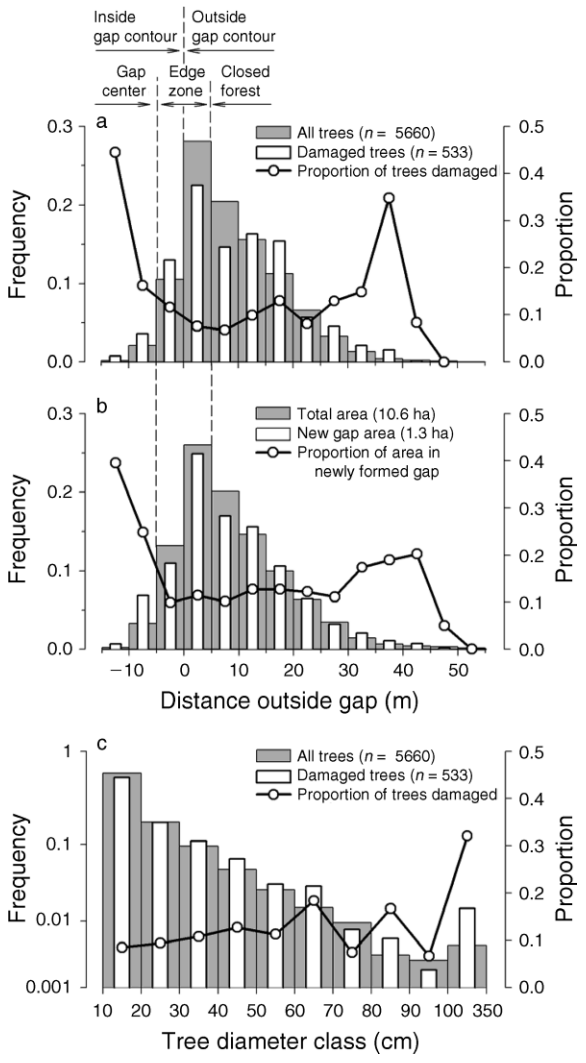


FIG. 2. Canopy disturbance over five years across 10.6 ha of tropical rain forest at Nouragues, French Guiana. (a, b) Cumulative incidence of (a) major tree damage and (b) new gap area, as a function of distance to the nearest contour of a preexisting gap. (c) Cumulative incidence of major tree damage as a function of tree diameter. Note that the *y*-axis in panel (c) uses a log scale.

between disturbance magnitude around existing gaps and the size of those gaps, which is in agreement with hypothesis 4.

## DISCUSSION

This study is the first individual-tree-based test of the hypothesis that canopy disturbances are spatially contagious in tropical rain forest. Individual-tree-based testing allowed us to directly test whether the risk of tree fall around gaps was elevated, the hypothesized mechanism of contagious disturbance. Moreover, we separately considered the possibility of an elevated disturbance risk and an increased magnitude of disturbances.

Our analyses yielded no strong evidence for spatial contagiousness of canopy disturbance at our study site. The risk of canopy disturbance was not significantly elevated around gaps, in disagreement with hypothesis 1, and disturbances occurring around gaps did not have a significantly greater magnitude (or "severity") than disturbances occurring elsewhere, in disagreement with hypothesis 3. The disturbance levels at the end of the five-year survey were independent of the locations of gaps at the start of the survey, in terms of both cumulative tree damage and new gap area. The major determinant of canopy disturbance in this forest was tree diameter, not gap proximity.

Nevertheless, patterns of cumulative canopy disturbance across the survey did appear contagious at first sight. Many of the damaged trees were located nearby preexisting gaps, suggesting association of disturbance with gaps, but these numbers simply reflected the relatively high frequency of gap-exposed trees in the population. Likewise, much of the newly formed gap area was located around gaps, suggesting frequent gap expansion, but new gap area was proportional to the amount of study area located around gaps. And existing gaps had elevated levels of disturbance: repeat disturbance was common (see *Discussion: Repeat disturbance*). Yet, canopy disturbance events, damaged trees, and newly opened gap areas were relatively infrequent around gaps, which is in disagreement with our hypotheses.

### *Gap size*

Foresters have long been aware of the incidence of wind throw increasing with the size and proximity of felling clearings (Alexander 1964), suggesting that

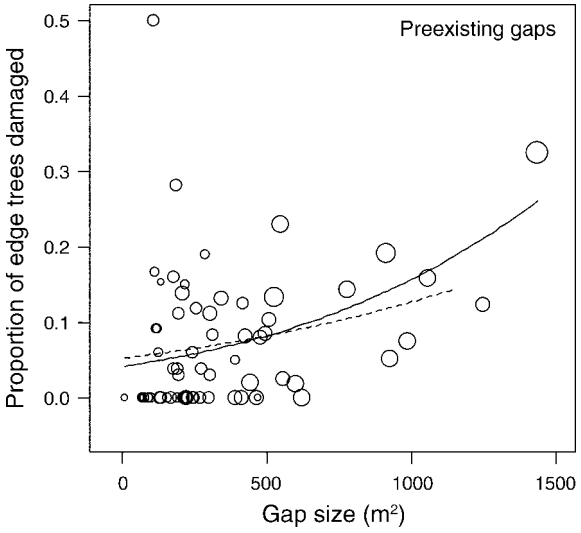


FIG. 3. Cumulative incidence of major tree damage over five years in the edge zones of different-sized preexisting gaps across 10.6 ha of tropical rain forest at Nouragues, French Guiana. Circle size is proportional to the number of trees exposed per gap. Lines are weighted logistic regression fits, including (solid line, $P < 0.001$) and excluding (dotted line, $P = 0.06$) the two largest gaps.

TABLE 2. Gap proximity and tree diameter as risk factors of canopy disturbance in tropical rain forest at Nouragues, French Guiana.

| Risk factor | RR ($e^{\beta}$) | 95% CI | $Z$ | $P$ | Sample size: No. trees | Sample size: No. tree years |
|---|---|---|---|---|---|---|
| a) Proximity continuous† | | | | | | |
| Tree diameter (cm)‡ | 37.0 | 20.6–72.9 | 11.4 | <0.001 | 5660 | 27 635 |
| Distance outside gap (m)‡ | 1.02 | 0.08–1.19 | 0.25 | 0.81 | 5660 | 27 635 |
| b) Proximity classification 1 | | | | | | |
| Tree diameter‡ | 34.0 | 19.6–61.3 | 12.3 | <0.001 | 5660 | 27 635 |
| Gap center§ | 3.67 | 1.67–8.06 | 3.23 | 0.001 | 155 | 693 |
| Gap edge§ | 0.89 | 0.63–1.25 | 0.70 | 0.49 | 2967 | 12 804 |
| Closed forest | 1.00 | | | | 3336 | 14 137 |
| c) Proximity classification 2 | | | | | | |
| Tree diameter (cm)‡ | 33.2 | 17.9–61.8 | 11.1 | <0.001 | 5660 | 27 635 |
| Inside gap§ | 1.56 | 0.94–2.59 | 1.72 | 0.09 | 1017 | 4278 |
| Gap-bordering§ | 1.03 | 0.66–1.59 | 0.12 | 0.91 | 663 | 2720 |
| Outside gap | 1.00 | | | | 4472 | 20 637 |

*Notes:* The relative risk (RR) of trees initiating a canopy disturbance event was estimated by robust Cox proportional hazards modeling with gap proximity as a time-dependent covariate and stem diameter as a fixed covariate. Risks are shown for three alternative measures of gap proximity. Blank cells indicate that no data are possible. β is the regression coefficient for the different explanatory variables.

† Includes only trees located ≥0 m outside gaps.

‡ Values are $\log_{10}$-transformed. RR is for one unit increase in the transformed value.

§ RR for proximity classes is in comparison with forest trees (classification 1) or trees outside gap contours (classification 2).

spatial contagiousness increases with gap size. Dale et al. (1986) suggested that a single large disturbance, through contagiousness, could cause long-term, complex dynamics of forest composition. Thus, the creation of large artificial openings by anthropogenic disturbances, such as shifting cultivation, logging and road building, could boost canopy disturbance of the surrounding forest and push these forests into a state of hyperdynamism (Dale et al. 1986, Laurance 1997). Several studies have observed elevated tree mortality along tropical forest edges (Williams-Linera 1990, Bierregaard et al. 1992, Laurance et al. 1998), but others have not (Laurance 1997, Turton and Freiburger 1997).

There was some tendency of the magnitude of canopy disturbances around gaps to increase with gap size: disturbance events occurring adjacent to larger gaps tended to involve more damaged trees and more tree falls than events occurring along smaller gaps, in agreement with hypothesis 4. These effects, however, were weak in comparison with the effects of tree diameter on disturbance magnitude, and did not result in elevated disturbance levels around gaps at the end of the study period. However, the canopy gaps in our study area were all natural and relatively small; all were <1500 $m^2$. This means that we cannot rule out that gap size becomes an important risk factor and a driver of spatial contagiousness in tropical forests once the size of gap openings surpasses a certain scale. Future studies should test whether canopy dynamics in these forests become spatially contagious after large-scale disturbances such as from hurricanes or humans, and enough to push forests into hyper-dynamism.

### *Repeat disturbance*

While gap-edge zones had relatively low disturbance levels, canopy disturbance levels were clearly elevated in gap centers. These high rates of "repeat disturbance" in the study area match the results of an earlier study in our study area by Van der Meer and Bongers (1996*a*), who found that 58% of 37 canopy gaps were re-

TABLE 3. Gap size and tree diameter as risk factors for canopy disturbance inside and around gaps in tropical rain forest at Nouragues, French Guiana.

| Initiator location | Gap size ($m^2$)†: RR ($e^{\beta}$) | 95% CI | $Z$ | $P$ | Tree diameter (cm)†: RR ($e^{\beta}$) | 95% CI | $Z$ | $P$ | Sample size: No. trees | Sample size: No. tree years |
|---|---|---|---|---|---|---|---|---|---|---|
| a) Gap edge zone | 1.58 | 0.74–3.36 | 1.18 | 0.24 | 32.6 | 15.0–71.0 | 8.80 | <0.001 | 2967 | 12 804 |
| b) Gap-bordering | 1.38 | 0.48–3.95 | 0.60 | 0.55 | 28.0 | 8.0–98 | 5.19 | <0.001 | 663 | 2720 |
| c) Gap center | 1.53 | 0.09–232 | 0.77 | 0.44 | 0.90 | 0.01–120 | 0.04 | 0.97 | 155 | 693 |
| d) All gap-exposed trees | 1.97 | 0.95–4.08 | 1.82 | 0.07 | 23.9 | 11.3–50.6 | 8.31 | <0.001 | 3113 | 13 498 |

*Note:* Rows represent Cox proportional hazards model fits for different subsets of the tree population. See Table 2 for further explanation.

† Values are $\log_{10}$-transformed.

TABLE 4. Relationship between gap proximity and the magnitude of canopy disturbances in tropical rain forest at Nouragues, French Guiana.

| Variable | No. of trees damaged | | | No. of trees fallen | | |
|---|---|---|---|---|---|---|
| | β† | *F* | *P* | β | *F* | *P* |
| a) Proximity continuous ($n = 88$ events)‡ | | | | | | |
| Tree diameter (cm)§ | 2.95 | 16.3 | <0.001 | 3.85 | 54.1 | <0.001 |
| Distance outside gap (m)§ | −0.44 | 1.14 | 0.29 | −0.13 | 0.13 | 0.72 |
| b) Proximity classification 1 ($n = 139$) | | | | | | |
| Tree diameter§ | 1.70 | 9.58 | <0.001 | 2.43 | 37.1 | <0.001 |
| Proximity class | | 0.23 | 0.79 | −2.13 | 1.52 | 0.22 |
| c) Proximity classification 2 ($n = 139$) | | | | | | |
| Tree diameter (cm)§ | 1.79 | 9.80 | 0.002 | 2.62 | 684 | <0.001 |
| Proximity class | | 0.68 | 0.51 | −2.46 | 36.7 | 0.09 |

*Note:* Two measures of disturbance magnitude were separately analyzed by generalized linear modeling for each of three alternative measures of gap proximity, with the stem diameter of the initiator as a fixed covariate.

† β for proximity classes is in comparison with forest trees (classification 1) or trees outside gap contours (classification 2).

‡ Excludes all trees located within gap contours.

§ Values are $\log_{10}$-transformed.

disturbed during three years. Repeat disturbance has been reported in many tropical forest studies and has been interpreted as spatial contagiousness of canopy disturbance (Martinez-Ramos et al. 1988, Young and Hubbell 1991, Van Der Meer and Bongers 1996*b*). Our results indicate that a high frequency of repeat disturbance does not necessarily imply contagiousness of disturbance. Repeat disturbance in our study was due to an elevated disturbance risk for trees inside gap centers, not to an elevated disturbance risk of trees

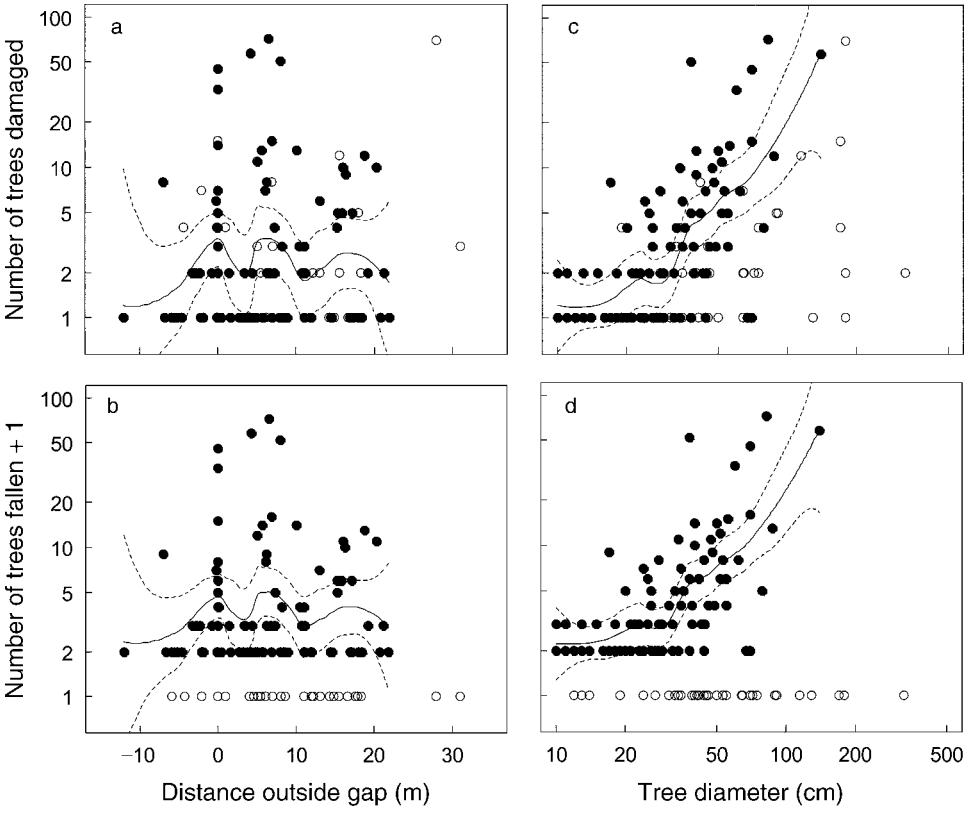


FIG. 4. Relationships between the magnitude of canopy disturbance events and (a, b) gap proximity and (c, d) initiator diameter at Nouragues tropical rain forest, French Guiana, for two different measures of magnitude. Solid circles are events initiated by tree falls ($n = 97$); open circles are events initiated by limb falls ($n = 42$). Spline functions are local polynomial regression estimates with 95% confidence intervals (dotted lines) showing trends for events initiated by tree falls, uncorrected for covariates. Full analyses are shown in Table 4.

TABLE 5. Relationship between gap size and the magnitude of canopy disturbances in tropical rain forest at Nouragues, French Guiana.

| Variable | No. of trees damaged | | | No. of trees fallen | | |
|---|---|---|---|---|---|---|
| | β | *F* | *P* | β | *F* | *P* |
| a) Gap edge trees ($n = 62$ events) | | | | | | |
| Gap size ($m^2$) | 1.54 | 5.17 | 0.03 | 1.01 | 4.21 | 0.04 |
| Tree diameter (cm) | 1.80 | 5.57 | 0.02 | 1.93 | 13.7 | <0.001 |
| b) Gap-bordering trees ($n = 32$) | | | | | | |
| Gap size ($m^2$) | 2.20 | 7.25 | 0.01 | 1.19 | 3.91 | 0.06 |
| Tree diameter (cm) | 0.03 | 0.06 | 0.81 | 0.77 | 0.46 | 0.50 |
| c) Gap-center trees ($n = 7$) | | | | | | |
| Gap size ($m^2$) | 6.72 | 2.37 | 0.20 | 5.45 | 2.93 | 0.16 |
| Tree diameter (cm) | −1.51 | 0.18 | 0.69 | −1.47 | 0.18 | 0.69 |

*Note:* Two measures of disturbance magnitude were separately analyzed by generalized linear modeling for events initiated by trees in three different proximity classes, with the stem diameter of the initiator as a fixed covariate. All data have been $\log_{10}$-transformed.

around gaps, the mechanism of spatial contagiousness. High disturbance levels inside gaps may largely reflect a delayed breakdown of trees that initially survive gap formation but fall later due to damage inflicted (Putz and Chan 1986). Arguably, such delayed damage may be considered part of the same gap-forming disturbance.

Our results resemble an earlier study in which repeat disturbance of gaps in a temperate deciduous forest in the Southern Appalachian mountains, USA, was monitored during four years (Runkle 1984). Like our study site, this forest also had small-scale gaps and a low incidence of hurricanes, fire, or other large-scale disturbance agents. There, 11% of the gaps had enlarged because peripheral canopy trees fell, and as many as 31% of the gaps had enlarged because surrounding trees died off. Nevertheless, mortality did not differ between gap-edge trees and overstory trees in general, indicating that gap presence did not influence mortality rates of trees around gaps (Runkle 1984). Repeat disturbance of small-scale gaps seems a largely endogenous process and should perhaps be regarded as a single staggered disturbance event.

### *Gap edges and seedling recruitment*

An apparent tendency of tropical-forest gaps to expand due to contagious disturbance (Foster and Reiners 1986, Hubbell and Foster 1986, Lawton and Putz 1988) led Schupp et al. (1989) to hypothesize that the edges of maturing gaps offer relatively favorable prospects for seedling regeneration, growth, and survival, particularly for small-seeded, shade-intolerant tree species. Our results indicate that gap edges in the Nouragues rain forest did not experience higher disturbance levels than closed-forest sites, unlike gap edges in temperate-zone forests (Worrall et al. 2005). The seeds and seedlings with the best prospects of being present where a new canopy opening is formed were probably those located inside existing gaps or away from existing gaps, rather than those in gap edges. The best locations may be areas with relatively high abundances of large trees, hence old forest patches, because large trees are more likely to initiate disturbances and which cause larger disturbances hence potentially larger gap openings (Brokaw 1982*b*).

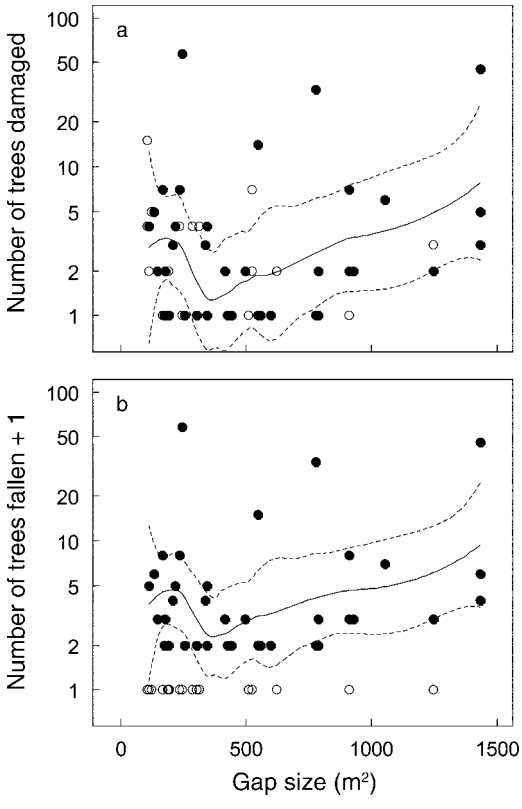


FIG. 5. Relationships between the magnitude of canopy disturbance events around gaps and gap size at Nouragues tropical rain forest, French Guiana, for two different measures of magnitude. Solid circles represent events initiated by tree falls ($n = 48$), open circles represent events initiated by limb falls ($n = 21$). Spline functions are local polynomial regression estimates with 95% confidence intervals (broken lines) showing trends for events initiated by tree falls uncorrected for covariates. Full analyses are shown in Table 5.

### *Gap-bordering trees*

Two previous studies (Young and Hubbell 1991, Young and Perkocha 1994) showed that gap-bordering trees developed more crown asymmetry, and that trees with asymmetrical crowns were more likely to fall. Young and Perkocha reasoned that trees growing adjacent to gaps, in combination with increased exposure to winds (Alexander 1964, Sprugel 1976, Foster and Reiners 1986), would be more likely to fall, but this hypothesis was never actually tested. Our study yielded no evidence for an elevated disturbance risk among a large number of gap-bordering trees at the Nouragues rain forest: gap-bordering trees were not more likely to fall than closed-forest trees of comparable dbh. This result suggests that any destabilizing effects associated with wind exposure and crown asymmetry at our study site were either unimportant or were counter-balanced by positive effects of gap proximity on tree growth and survival (e.g., Pedersen and Howard 2004). For example, above- and below-ground resources for tree growth are more abundant in gaps (Canham et al. 1990, Wilczynski and Pickett 1993), and trees inside and along gaps can exploit these resources to enhance their growth rates (Canham 1988), thereby reducing their vulnerability to disturbance. Another possible reason for the absence of an effect is that asymmetry increases particularly in shorter, sub-canopy trees that are overtopped by neighbors (Young and Hubbell 1991), while especially large individuals have a high impact when falling and may cause domino effects creating new canopy gaps (Van Der Meer and Bongers 1996*b*, this study).

### *Tree size as driver of canopy disturbance*

Tree diameter was the major risk factor for trees initiating a disturbance event and the major determinant of the magnitude of disturbances. This result is in line with the idea that tree mortality increases with tree age—trees become more susceptible to random disturbance as they get older (Runkle 1985*b*, Lorimer et al. 2001)—and with earlier studies suggesting that tree size largely determines disturbance magnitude (e.g., Brokaw 1982*a*). Our study shows that these two effects of tree size add up, and that tree size is the major factor driving canopy disturbance in our study area. Disturbance levels may thus be higher in older forest patches, where large trees are most common (Brokaw 1982*b*, Lorimer 1989). Our findings are consistent with the traditional view of tropical rain forests as mosaics of patches with predictable regeneration cycles (Aubréville 1938, Richards 1952), but perhaps independent of where disturbances previously occurred.

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